VESSELS OF THE GNETALEAN TYPE IN ANGIOSPERMS[1]

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(WITH PLATES XXIX–XXXII)

A common feature of Gnetales and Angiosperms is the possession of true vessels. The evolution of the vessel perforation and its typical form have long been matters of investigation. THOMPSON[2] has stated recently that the derivation and evolution of the vessel in Gnetales is distinct and different from that found in Angiosperms. On the other hand, SOLEREDER[3] and DEBARY[4] mention the existence among certain Angiosperms of the peculiar bordered pore which THOMPSON so definitely limits to the Gnetales. The present investigation, which covers a number of species of Angiosperms and Gnetales, confirms and extends the observations of SOLEREDER and DEBARY on Angiosperms and of THOMPSON on Gnetales. The writer finds it necessary, however, to differ from the conclusions of THOMPSON on Angiosperms.

Gnetales

In *Ephedra*, the lowest genus of Gnetales, primitive conditions of vessel organization are found. Fig. 1 is a section of wood taken in a primitive region near the pith. To the extreme left are the long slender tracheids with their characteristic pits, bordered and containing a torus. In the center are two large vessels which, in their several ways, show a distinct relation to and evolution from the tracheid condition. The vessel more to the left has pits of ordinary tracheary type at either end, except that they are somewhat enlarged in the vessel condition, but retain both border and

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

[2] THOMPSON, W. P., Independent evolution of vessels in Gnetales and Angiosperms. BOT. GAZ. 65:83–90. 1918.

———, Anatomy and relationships of the Gnetales. 1. *Ephedra*. Ann. Botany 26:1077-1104. 1912.

[3] SOLEREDER, HANS, Systematische Anatomie der Dicotyledonen, Stuttgart. 1899.

[4] DEBARY, H. A., Comparative anatomy of the vegetative organs of the Phanerogams and Ferns. Trans. by F. O. BOWER and D. H. SCOTT. Oxford. 1884.

torus. In the center of the same vessel, passing upward from the lower end, is one pit which retains its border but has lost the torus and membrane. The center of this vessel shows as many as five perforations which have gone a long way in evolution and have lost both membrane and torus. It is to be concluded that these are perforations highly specialized to carry on the vascular function. The vessel to the right has a precisely similar condition at either end, namely enlarged tracheary pits. Toward the center of this vessel from top or bottom are three pits in the first case, and two in the second which retain border and torus, but have reached distinctly the size characteristic of vessels. The eight more central pits retain a definite border, but each shows an absence of membrane and torus. This vessel is obviously less specialized, and therefore less efficient than the one previously considered; nevertheless it shows marked progress in the line of development. To the extreme right are typical tracheids, once again proving that these two vessels occur side by side with the elements from which they originate.

In *Gnetum*, the highest genus of Gnetales, conditions are especially interesting. Fig. 2 shows a longitudinal section, in rather low magnification, taken from the medullary region. The first vessel to the left has pits of the tracheary type at its top. These are many, crowded, and retain border and membrane, there being usually no torus in *Gnetum*. Toward the center the pits are somewhat enlarged, although still retaining the border. In the region of the perforation of the vessel there is a group of seven pits. These are distinctly larger than those on the side wall of the vessel and larger than those of most tracheids, and their borders are still distinct. The most interesting feature of this group, however, is found in the two lowest pits whose adjacent borders have broken down and show well defined fusion. This is the first example of pit fusion to be described, and is clear and convincing. Moreover, this is obviously a step higher than the conditions found in *Ephedra*, and foreshadows the more extensive fusion of pits to form a single large opening, which is the natural outcome from such conditions. In the same figure to the right are two large vessels in series. The higher vessel shows a large perforation resulting from pit fusion.

About this perforation is a well defined border, and except for a vestige of a cross wall that runs into it from the left, we should find here the simple large open perforation which is the result of complete fusion; in other words, the type characteristic of the more advanced species of *Gnetum*. The vessel below shows an imperfect perforation resulting from the more or less complete fusion of a number of large open bordered pits.

Fig. 3 presents a higher magnification of two large vessels, the one to the extreme left showing a group of four large tracheary pits arranged suggestively for fusion. To the right is a vessel with a single large opening as its perforation, this being the typical condition in more advanced species of *Gnetum*. The border is distinct, and by its slightly irregular outline, which shows especially well at the upper right side of the perforation, reveals its origin from a type like the vessel on the left in the same figure. Fig. 4 is a high magnification of an intermediate stage of fusion, showing the remains of a transverse process about to disappear.

Angiosperms

In Angiosperms the evolution of the vessel from the tracheid proceeds along the same lines as in Gnetales. Fig. 5 shows the organization of the mature wood in *Alnus japonica*. Here is seen the scalariform perforation characteristic of the Betulaceae and other presumably primitive Angiosperms. The pits, which are many and crowded, have fused in horizontal rows to form scalariform pits. The condition is seen even more clearly to be decidedly scalariform under higher magnification, as in fig. 6.

A section through the medullary region of *Alnus japonica* is shown in fig. 7. This is a rather low magnification, but shows clearly the primitive spiral and scalariform tracheids to the left. The three vessels to the right of these tracheids show all transitional stages from small pits to the scalariform perforations. The occurrence of this form of vessel perforation side by side with scalariform tracheids proves that it is indeed a primitive type for this genus of the woody Angiosperms. Fig. 8 shows these same vessels and tracheids under higher magnification. Fig. 9 is still another

high magnification of a vessel in *Alnus japonica*, in which the origin of the scalariform perforation from fusions of rows of pits is clear and convincing.

We pass now from woody Angiosperms to the consideration of the herbs and vines among Angiosperms, which in their vascular structures more closely resemble the conditions found in *Gnetum*, and show stages of perforation strikingly like those found in that genus. Fig. 10 is a section through the wood near the pith of *Potentilla palustris*. Several vessels are shown in the figure with a rather advanced development of the scalariform pits in the region of perforation. This condition resembles that found in the mature wood of *Alnus*. Fig. 11 is a section taken from the medullary region of *Potentilla monspeliensis*, an annual species. To the left are the characteristic spiral and scalariform tracheids of the protoxylem, and to the right are vessels with scalariform perforations on the end wall. Of these vessels, the one to the right shows a tendency at its lower end toward fusion of the scalariform pits. To the extreme right of the same figure is a vessel, low in the field, with the single large bordered pore characteristic of the mature wood of *Potentilla* as well as of the vessels of *Gnetum*. A further example of the close relation to the Gnetalean pitting is found in fig. 12, another section of the wood of *Potentilla monspeliensis*. To the left are two vessels in series. Both have the small pits grouped for fusion as in *Ephedra* and in certain species of *Gnetum* (figs. 1–3); in fact several of the pits have already fused in the higher vessel. To the extreme right is a vessel with a large *Gnetum*-like pore. Fig. 13, another section of *Potentilla monspeliensis*, shows three other vessels in the region of perforation. The vascular element to the left has again *Ephedra*-like pits grouped and fusing. The two vessels to the right in series have a curious *S*-shaped fusion of pits, quite out of keeping with any mode of origin save a haphazard union of pits. Fig. 14 shows part of the same field under higher magnification. It is clear that the two vessels here manifest the process of fusion of numbers of small pits. Fig. 15 is a high magnification of a similar condition in the same genus. Examples of like conditions might be indefinitely multiplied from

the study of this and other species of *Potentilla*. From the mode of perforations found in *Potentilla* it is seen that both the scalariform type and the *Gnetum*-like type, resulting from haphazard fusion, occur side by side and sometimes in the same species. It thus appears that both *Ephedra* and *Gnetum*-like types of perforation occur in this instance, and undoubtedly the bordered open pore has originated here from the grouped pits, either by horizontal or haphazard fusions. The possession of the scalariform type of perforation thus loses significance as a phylogenetic criterion and has only the importance of an anatomical detail. Further, the open bordered pore has often the same derivation in *Potentilla* and in other herbaceous Rosaceae as the similar bordered pore in *Gnetum*.

We pass now to the Geraniales, a group systematically remote from the Rosaceae. Fig. 16 shows a longitudinal section of the wood of *Pelargonium*. In the center is the region of perforation of a vessel, showing the bordered pore typical of the more advanced species of *Gnetum*. Even the border is clearly evident, a condition which THOMPSON apparently has failed to observe as occurring in the so-called porous perforation characteristic of the vessels of many Angiosperms, particularly (although not exclusively) those of herbaceous and liana-like habit. Fig. 17 shows another vessel of *Pelargonium* which illustrates an *Ephedra*-like perforation in this genus. There is obviously no difference here from the vessel perforation found in *Ephedra* except that the pits are small and both torus and membrane are always absent. There is no reason to believe that these pits are to fuse to form scalariform perforations, rather there is every evidence to infer a prospective haphazard fusion from the two or three instances of union manifested along the lower border of the perforation. This type precedes the open pore of fig. 16. Additional proof of this conclusion is supplied in fig. 18 from the same genus (*Pelargonium*). The vessel to the left has an interesting perforation. Small pits in the process of fusion surround an open bordered pore. When fusion is complete the enlargement of the central bordered porous opening will result. In the vessel adjacent to this is the large open bordered pore characteristic of the vessels of the Geraniales, and below it is

another similar perforation. Fig. 19 shows a higher magnification of the same vessel as presented in fig. 18. The details of border in the large central pore demonstrate the existence in Angiosperms of the *Gnetum*-like pore. Fig. 20 illustrates another vessel of *Pelargonium* showing two perforations in series. The upper perforation manifests a transitional stage of fusion. The high degree of magnification furnishes undoubted evidence that the complete fusion of pits will result in a large bordered perforation precisely as in *Gnetum*. Below is a bordered porous perforation.

Fig. 21 shows the partially pitted perforation of another vessel of *Pelargonium*. Fusion for the most part has already taken place, but enough small pits remain to establish a definite origin of the open bordered pore by *Gnetum*-like haphazard fusion. Fig. 22 shows a scalariform perforation in the same species of *Pelargonium*. The existence of this type, together with the bordered perforation derived from the fusion of *Ephedra*-like terminal pits, illustrated in the Rosaceae, shows again that the scalariform type of perforation is not exclusively present in or solely characteristic of Angiosperms. There is undoubted similarity between perforations of the Rosaceae and the Geraniales and those obtaining in *Gnetum* itself.

Fig. 23 shows two interesting vessels of the wood of *Tropaeolum* as a further illustration of the Geraniales. Both vessels have the *Ephedra*-like grouping of pits, although the size is obviously smaller than in that genus. Close scrutiny reveals the fusion to be haphazard-oblique and marginal, and not resulting in horizontal scalariform perforations. Most of the vessels in *Tropaeolum* have the *Gnetum*-like bordered terminal pore. Fig. 24 shows a section through the wood of *Clematis* species, an example of the Ranunculaceae. The margin of an open bordered perforation is shown, and around its inner edge is seen a fringe of haphazardly fusing pits. Vessels of the *Gnetum* type are practically universal in the Ranunculaceae.

Conclusions

Conditions similar to those illustrated for the Rosaceae, Geraniales, and Ranunculaceae are widespread among dicotyledonous Angiosperms, particularly those of herbaceous and climbing habit.

It seems unnecessary to exemplify further the occurrence of perforations identical with those characteristic of the Gnetales in the Angiosperms, since the examples furnished, which could be indefinitely multiplied, show that the vessels of Angiosperms can and often do originate precisely as in the highest group of the Gymnosperms, the Gnetales. It accordingly appears clear that THOMPSON'S assumption of a distinct origin for the Gnetales on the basis of a different mode of derivation of their vessels falls to the ground. This author has pointed out that the types of rays found in the Gnetales are strikingly similar in their mode of origin to those of the Angiosperms. He has further recently drawn attention to the nuclear fusions in the embryo sac of *Gnetum*, which he compares with the well known nuclear fusions in the female gametophyte of Angiosperms. It would appear, therefore, that far from demonstrating by his description of the mode of origin of vessels in *Gnetum* the separate derivation of the Angiosperms from the Gnetales, in reality this author has furnished additional conclusive evidence of their descent from a common stock. It is apparently clear from the present investigation that many herbaceous and vinelike Angiosperms, from the lowest to the highest groups, show types of vessel perforation identical with those found in the usually vinelike *Gnetum*. Even the Monocotyledons manifest very commonly the *Gnetum* type of vessel, which is further quite universal in the Compositae.

Summary

1. Vessels with scalariform perforations of the angiospermous type and bordered porous perforations of the *Gnetum* type occur side by side in the Rosaceae, being found even in the same species of *Potentilla*.

2. Similar observations are recorded for the Geraniales and Ranunculaceae, and these might be indefinitely multiplied from other herbaceous Angiosperms.

3. Recent statements that the types of vessels in the Gnetales and Angiosperms are distinct in their mode of derivation are accordingly without foundation in fact.

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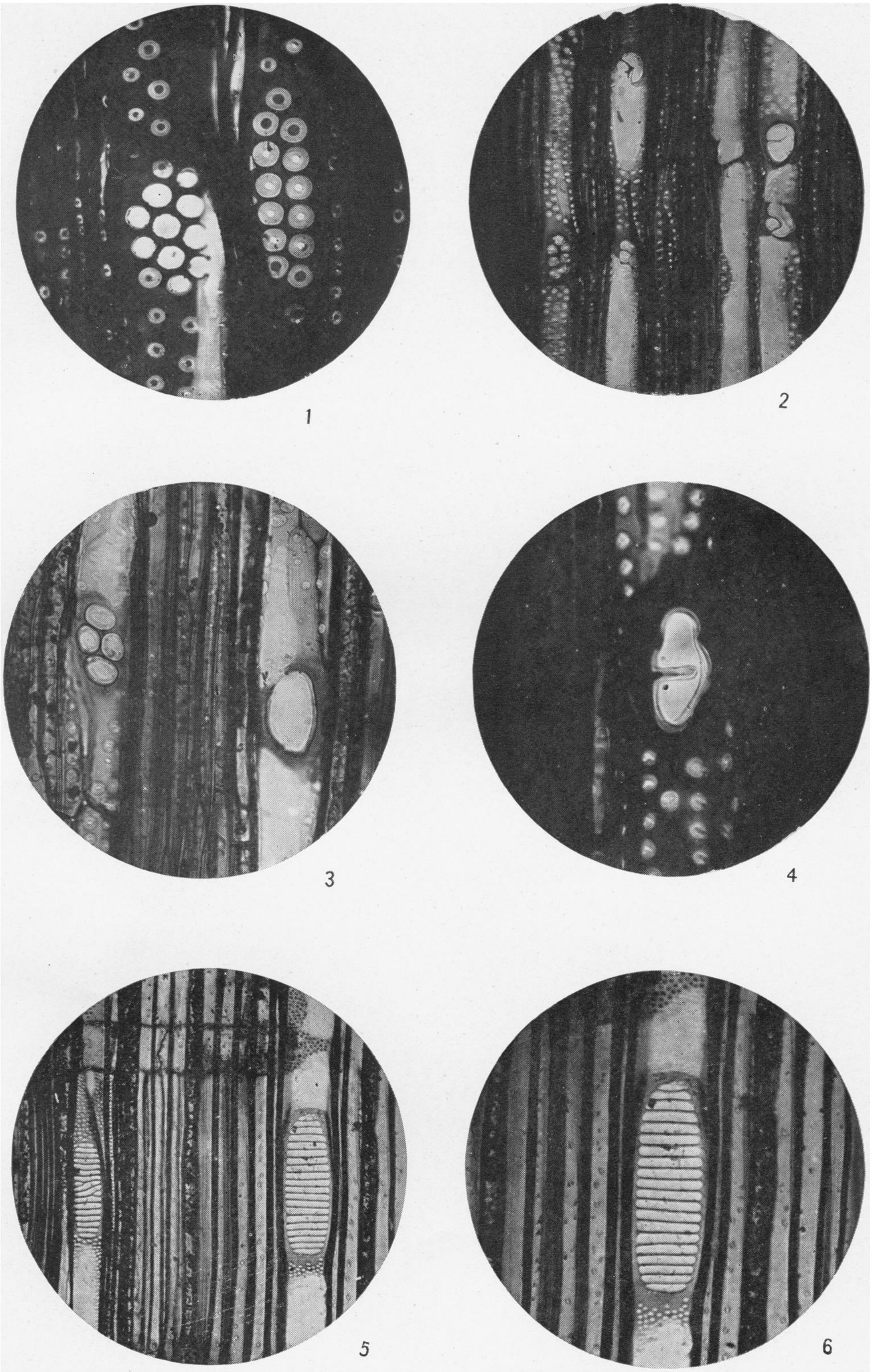

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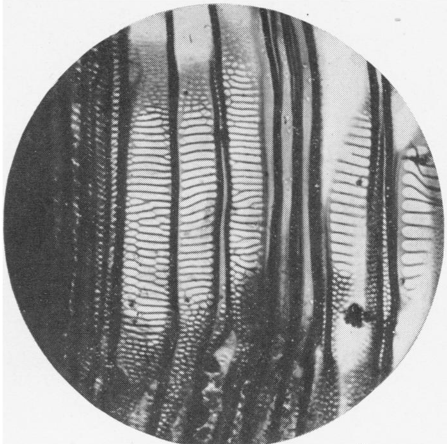

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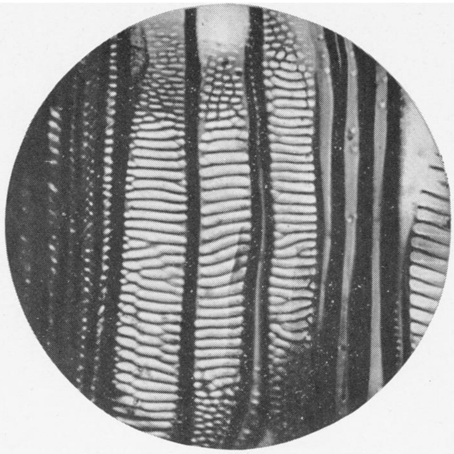

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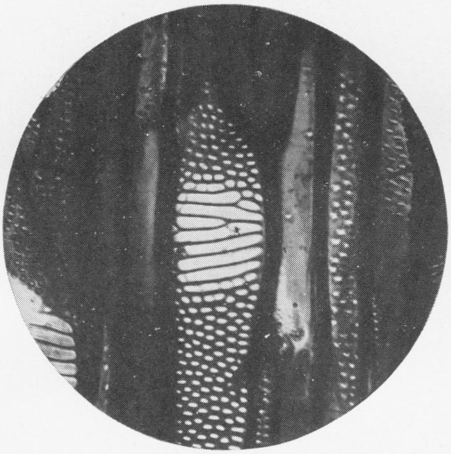

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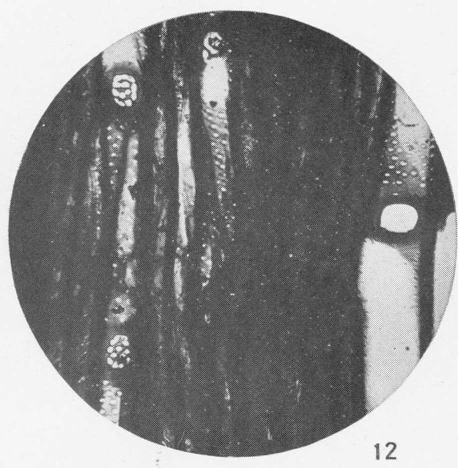

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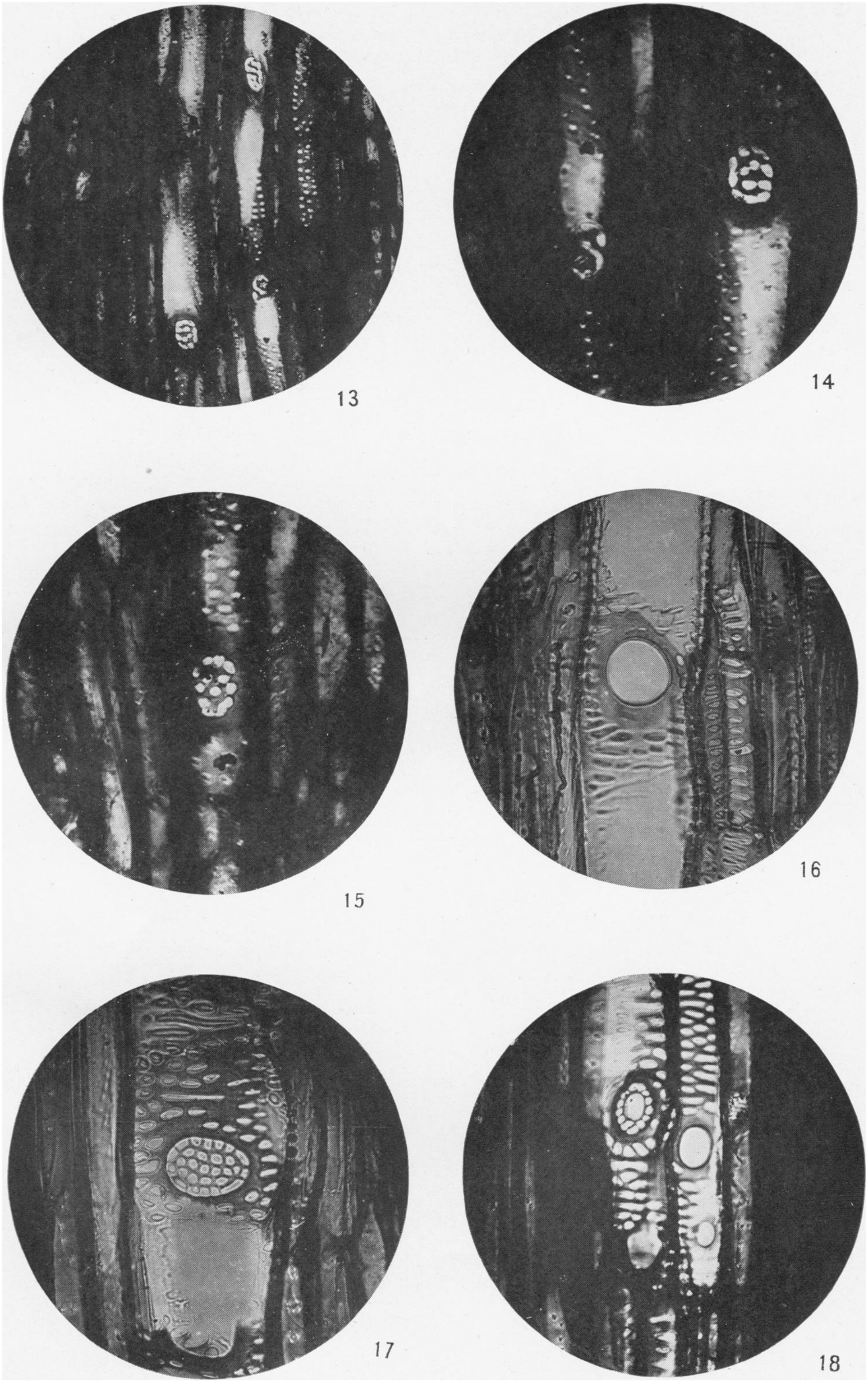

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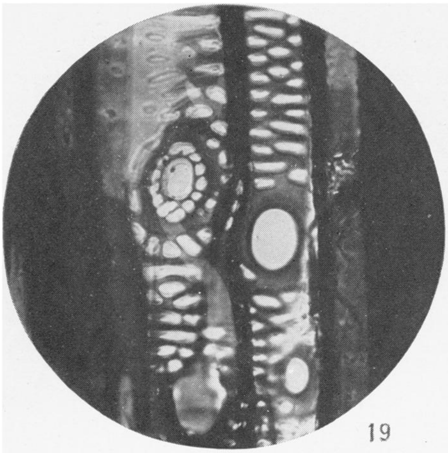
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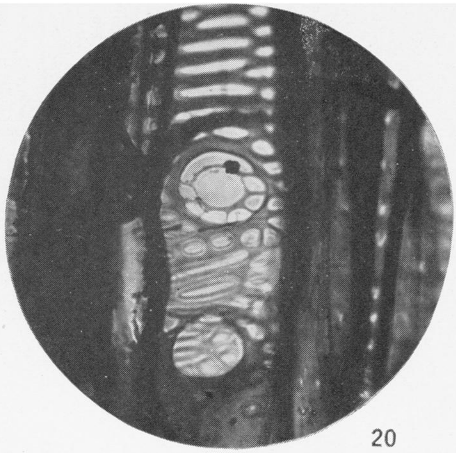
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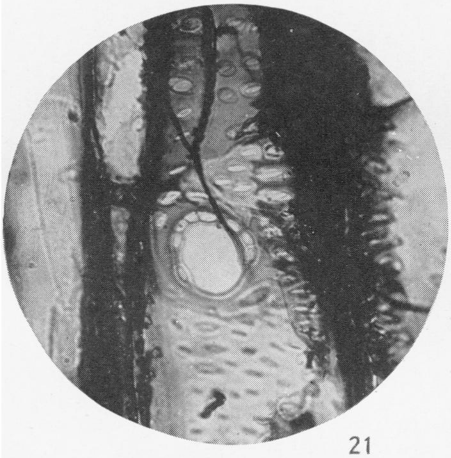
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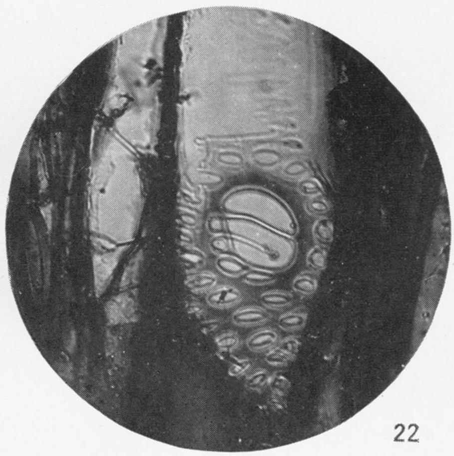
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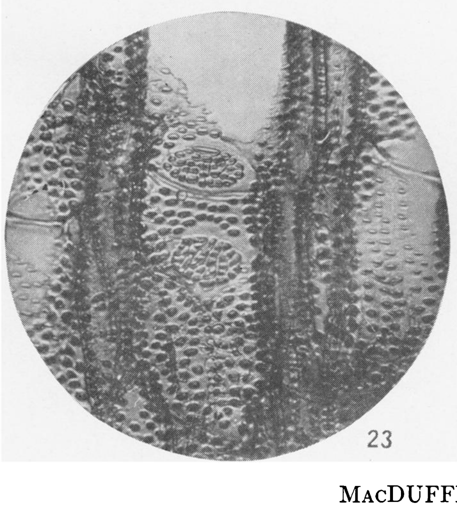
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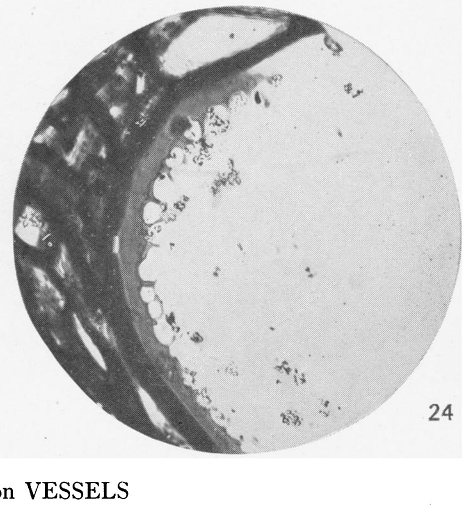
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EXPLANATION OF PLATES XXIX–XXXII

PLATE XXIX

FIG. 1.—Radial section of wood of *Ephedra trifurca;* ×300.
FIG. 2.—Radial section of wood of *Gnetum* sp.; ×150.
FIG. 3.—Radial section of wood of *Gnetum* sp.; ×300.
FIG. 4.—Radial section of wood of *Gnetum* sp.; ×400.
FIG. 5.—Radial section of mature wood of *Alnus japonica;* ×200.
FIG. 6.—Radial section of mature wood of *Alnus japonica;* ×300.

PLATE XXX

FIG. 7.—Radial section of wood of *Alnus japonica* near pith; ×200.
FIG. 8.—Radial section of wood of *Alnus japonica* near pith; ×300.
FIG. 9.—Radial section of vessel of *Alnus japonica* near pith; ×400.
FIG. 10.—Radial section of wood of *Potentilla palustris* near pith; ×300.
FIG. 11.—Radial section of wood of *Potentilla monspeliensis* near pith; ×300.
FIG. 12.—Radial section of wood of *Potentilla monspeliensis;* ×200.

PLATE XXXI

FIG. 13.—Radial section of wood of *Potentilla monspeliensis;* ×200.
FIG. 14.—Radial section of lower part of same more highly magnified; ×400.
FIG. 15.—Radial section of another vessel of same species; ×400.
FIG. 16.—Radial section of vessel of *Pelargonium* sp.; ×400.
FIG. 17.—Radial section of *Ephedra* or *Gnetum*-like vessel perforation in *Pelargonium* sp.; ×400.
Fig. 18.—Radial section showing two vessels of *Pelargonium* sp.; ×200.

PLATE XXXII

FIG. 19.—Radial section of wood of *Pelargonium* sp., showing same two vessels more highly magnified; ×400.
FIG. 20.—Radial section of another vessel of same species; ×400.
FIG. 21.—Radial section of another vessel of same species; ×400.
FIG. 22.—Radial section of another vessel of same species; ×400.
FIG. 23.—Radial section of wood of *Tropaeolum* sp.; ×400.
FIG. 24.—Transverse section of wood of *Clematis* sp.; ×500.